

The *Solenopsis saevissima* Complex in South America (Hymenoptera: Formicidae)

by

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Solenopsis (Solenopsis) saevissima (F. Smith) is one of the most variable and widespread species of the South American ant fauna, and it has consistently presented some of the more knotty problems of ant taxonomy. The difficulties involved in its delimitation were compounded during the period 1904-1936 by a plethora of intraspecific forms erected by FOREL and SANTSCHI, neither of whom ever were able to gain an over-all picture of the variation with which they were dealing. Most of their forms were questionable or of dubious relationships from the very beginning. A major step toward the clarification of this matter was made by CREIGHTON, who in 1930 synonymized seven of the sixteen recognized names. In the light of modern systematics this was still a very conservative move, because of the nine names which he left standing only two occupied extensive exclusive ranges and most were concentrated in a broad belt extending from southern Brazil through northern Argentina. On the basis of distribution alone most of these forms are suspect, an opinion which CREIGHTON himself has recently expressed (*in litt.*).

The following revisional study of the *Solenopsis saevissima* complex has been undertaken as an extension of the study of variation in the introduced population of *S. saevissima* in the Gulf States (WILSON, 1951). It has been made possible only through the generous help of several American entomologists, including Dr. NICOLAS KUSNEZOV of Argentina (Fundación Miguel Lillo, Tucumán), Monsignor THOMAS BORGMEIER of Brazil, and Dr. HARRY MARCUS of Bolivia. These three men loaned to me a total of many thousands of specimens representing over 250 nest series collected at 80 localities. I wish to express my sincere appreciation to them; it is indeed gratifying to know that such large collections have been assembled and are available to interested specialists.

All three castes of *Solenopsis s. saevissima* (F. Smith) have been described in detail by CREIGHTON (1930) and the diagnostic characters of the subsequently recognized variants summarized. Those interested in the subgenus as a whole are referred to this work as a base reference.

In the present revision three species, one containing two subspecies, are recognized as valid.

KEY TO THE FORMS OF THE *SOLENOPSIS SAEVISSIMA* COMPLEX

1. Antenna of queen 10-jointed, the third funicular segment composed of the fused third and fourth segments and therefore longer than the second segment *Solenopsis pythia*
- Antenna of queen 10-jointed, the third funicular segment shorter than the second 2
2. Soldiers with alitrunks 1.6 mm - 2.2 mm in length; ground color light yellow to brownish yellow, the posterior margins of the gastric segments medium to piceous brown and contrasted sharply against the lighter anterior portions; queens with color similar to that of soldiers, their heads moderately cordate *Solenopsis interrupta*
- Soldiers with alitrunks at most 1.9 mm in length; ground color light yellow to piceous brown; the gaster variable, but at most only the first or second segments with the contrast pattern of *interrupta*; color of queens similar to that of soldiers, the heads quadrate 3
3. Color light yellow to brownish yellow, the gastric segments edged with light to medium brown; heads of the soldiers quadrate *Solenopsis s. saevissima*
- Color dark to piceous brown, often with a lighter patch on the dorsum of the first gastric segment; heads of the soldiers moderately cordate *Solenopsis s. richteri*

Solenopsis (Solenopsis) pythia Santschi

- 1934 *Solenopsis pythia* Santschi, Rev. Soc. Ent. Argentina, Vol. VI, n.º 1, pp. 30-31. Type locality: Loreto, Misiones, Argentina.

SANTSCHI was of the opinion that this species, which was described from a single queen, has its closest affinities to *S. saevissima* and *S. gayi*, so that placing it here in the *saevissima* complex is only a guess made for convenience. The fused third and fourth funicular segments should make it easily recognizable. According to SANTSCHI the eyes are larger than in related species and set very far forward on the head, almost touching the plerostomal sutures. The ground color is deep reddish yellow; the gaster is piceous brown, with a lighter patch on the first gastric segment. The remainder of SANTSCHI's description does not contain sufficient detail to make possible further critical comparisons. It is interesting to note that he considered that *pythia* might be a parasitic form derived from *saevissima*, and this is not entirely improbable. This species is apparently either rare or a cryptic, that is, distinguishable only by the queen caste, because it was absent from a large number of series which I examined from Misiones, including several from Loreto itself.

Solenopsis (Solenopsis) interrupta Santschi

- 1916 *Solenopsis saevissima* var. *interrupta* Santschi, Physis Buenos Aires, Vol. II, p. 397. Type locality: Bajo Hondo, Buenos Aires, Argentina.
- 1916 *Solenopsis saevissima* var. *macdonaghi* Santschi, Physis Buenos Aires, Vol. II, p. 397.

- 1916 *Solenopsis geminata* subsp. *pylades* Forel. Bruch, Rev. Mus. La Plata, Vol. XXIII, p. 313.
1930 *Solenopsis saevissima* subsp. *interrupta* Santschi. Creighton, Proc. Amer. Acad. Arts and Sci., Vol. LXVI, n.º 2, pp. 89-92.

The known range of this species is shown in figure 1. Its sibling relationship with *S. saevissima* adds confusion to the classification of the complex, so that series with color approaching that of *interrupta* are definitely determinable only if soldiers or queens are present. The diagnostic characters of this species are discussed in detail below.

1. The ground color ranges from pale yellow to dark reddish yellow, the appendages, alitrunk, petiole, postpetiole, and occiput frequently being darker than the remainder of the body. In the queens, soldiers, and larger medias the posterior margins of the first 3 or 4 gastric segments are characteristically piceous, giving a markedly striped appearance to the gaster not possessed by any known variant of *saevissima*. Material from MENDOZA (El Salto, Malargüe, Carrizal de Abajo) and from NEQUEN (Zapala) in the collection of the Fundación Miguel Lillo contains exceptionally light nest series, in which the gastric bands are little more than marginal infuscations. Material from Bolivia (Cochabamba and environs) contains series which are exceptionally dark, the anterior portions of the gastric segments being somewhat infuscate but still distinguishably lighter than the posterior margins. These color differences show no significant geographical delimitations; for instance relatively dark series were taken in Mendoza, and typically light forms are apparently common around Cochabamba. In general *interrupta* shows remarkably little color variation as compared to *saevissima*; the great majority of the numerous series examined were a clear yellow tending toward the lighter end of the variation.

2. All three castes of *interrupta* are larger and less variable in size than those of *saevissima*. A series of 20 *interrupta* queens selected at random from several localities had alitrunks ranging in length from 2.48 mm to 2.75 mm, with a mean of 2.61 mm; a similar lot of *saevissima* queens, including both subspecies and intergrades, showed variation from 2.11 mm to 2.59 mm, with a mean of 2.42 mm. A series of 20 *interrupta* males selected at random from several localities showed variation from 2.43 mm to 2.70 mm, with a mean of 2.55 mm; a similar lot of *saevissima* males showed variation from 2.24 mm to 2.67 mm, with a mean of 2.42 mm. A series of 20 *interrupta* soldiers selected at random from several localities showed variation from 1.65 mm to 2.13 mm, with a mean of 1.90 mm; a similar lot of *saevissima* soldiers showed variation from 1.27 mm to 1.89 mm, with a mean of 1.85 mm. All measurements were made from the base of the pronotal collar to the junction of the propodeum and petiole; maximum error was ± 0.02 mm. As a rule *interrupta* minors tend to be larger than *saevissima* minors, but it is probable that few of the series used in this study contained true minimas. There appears to be a north-south cline in size in the *interrupta* population, with the largest soldiers and queens originating from Bolivia. This may well fall into a subspecific pattern,

but it will have to be checked statistically with more material than is now available. If it does exist, it is just the reverse of that seen in *saevissima*.

3. The cordate condition of the heads of the *interrupta* queens can be more accurately described as a swelling of the posterior half of the head, so that the frontal diameter directly in front of the eyes is a little less than 1.2 times that directly behind the eyes. The heads of *saevissima* queens rarely approach this condition and can best be described as subquadrate.

Except for their larger size, *interrupta* males are apparently morphologically identical to *saevissima* males. This includes wing venation and genitalia as well as the usual features of external morphology.

From figures 1 and 2 it will be noted that the range of *interrupta* covers that of *saevissima richteri* and the western half of the *s. saevissima-s. richteri* blend zone. The specific distinctness of *interrupta* is supported by its relative uniformity throughout its range; it fails to show any sign of geographical variation corresponding to that of *saevissima*. In Bolivia and parts of northern Argentina (Jujuy, Salta, Formosa), where *saevissima* is quite small and shows distinctive local color variation, the disparity between the two species is very marked.

Possible additional evidence of the distinctness of these two species is to be seen in their mating seasons. Of 163 series of both species from Argentina loaned to me by Dr. KUSNEZOV, 28 contained winged forms. The times of their collections are summarized in the following table. If these data can be accepted as representing a trend, it appears that *saevissima* breeds primarily in the Argentine winter and *interrupta* in the summer. Much additional field work needs to be done, however, before this possibility can be tested.

	J	F	M	A	Maó	June	Juló	August	S	O	N	D
<i>Saevissima</i>	0	0	0	1	1	1	2	2	0	0	1	0
<i>Interrupta</i>	4	4	4	2	1	2	0	0	0	1	3	0

Solenopsis (Solenopsis) s. saevissima (F. Smith)

- 1855 *Myrmica saevissima* F. Smith, Trans. Ent. Soc. Lond., Vol. III, p. 166, pl. 13, fig. 18. Type locality: Trabajos River, Para, Brazil.
- 1862 *Solenopsis geminata* subsp. *rufa* (Jerdon). Mayr, Verh. Zool.-bot. Ges. Wien, Vol. XII.
- 1904 *Solenopsis moelleri* Forel, Ann. Soc. Ent. Belg., Vol. XLVIII, p. 173.
- 1904 *Solenopsis moelleri* var. *gracilior* Forel, *Ibid.*, p. 174.
- 1908 *Solenopsis geminata* var. *incrassada* Forel, Verh. Zool.-bot. Ges. Wien, Vol. LVIII, p. 362.
- 1909 *Solenopsis pylades* Forel, Ann. Soc. Ent. Belg., Vol. XLVIII, p. 172.

- 1914 *Solenopsis pylades* subsp. *electra* Forel, Bull. Soc. Vaud. Sci. Nat., Vol. I, p. 274.
- 1915 *Solenopsis geminata* subsp. *saevissima* (F. Smith). Wheeler, Bull. Amer. Mus. Nat. Hist., Vol. XXXIV, p. 397.
- 1915 *Solenopsis geminata* subsp. *saevissima* var. *incrassata* Forel. Wheeler, *Ibid.*, p. 397.
- 1915 *Solenopsis geminata* subsp. *electra* Forel. Wheeler, *Ibid.*, p. 397.
- 1916 *Solenopsis saevissima* (F. Smith). Santschi, Physis Buenos Aires, Vol. II, pp. 378-380.
- 1916 *Solenopsis saevissima* var. *incrassata* Forel. Santschi, *Ibid.* p. 380.
- 1916 *Solenopsis saevissima* var. *pylades* Forel. Santschi, Physis Buenos Aires, Vol. II, p. 380.
- 1916 *Solenopsis saevissima* var. *morosa* Santschi, *Ibid.*, p. 380.
- 1916 *Solenopsis saevissima* subsp. *electra* Forel. Santschi, *Ibid.*, p. 381.
- 1916 *Solenopsis saevissima* subsp. *electra* var. *wagneri* Santschi, *Ibid.*, p. 382.
- 1923 *Solenopsis saevissima* var. *perfidia* Santschi, Rev. Suisse Zool., Vol. XXX, p. 266.
- 1936 *Solenopsis saevissima* subsp. *oblongiceps* Santschi, Rev. de Ent., Vol. VI, pp. 405-406, fig. 5.

If this synonymy are included forms described from the *s. saevissima-s. richteri* blend zone as well as forms identical with the typical race. The distribution of the two subspecies is shown in figure 2. The exact status of many of the described forms have been exceptionally difficult to decide, principally because the entire *saevissima* population contains a complex north-south cline. Throughout northern and central Brazil and the Guianas the population is fairly homogeneous and is characterized by a clear yellow ground color. Also, the alitrunks of the minor workers are perceptibly thinner than those found further south, as pointed out by CREIGHTON. It is proposed here that this northern segment of the population be designated as the typical subspecies; this is approximately the same thing recognized by CREIGHTON in his 1930 revision. Further south, in the area covering extreme southern Mato Grosso to Santa Catarina, the ground color deepens to medium or even dark brown, but the original *saevissima* gastric pattern is retained. It was from this area that the var. *moelleri* was described. In the area encompassing Rio Grande do Sul through northern Argentina and north in the west at least to central Bolivia, the variation becomes erratic and affects size, body shape, and color, although the color remains approximately intermediate in the over-all clinal trend. It was from this area that most of the superficial subspecies and varieties were described. Further south, in central Argentina, the color deepens still more and becomes the main diagnostic character of the southern subspecies *saevissima richteri*. The distribution of the more easily recognized variants, including three which have not been formally named, is shown in figure 3, and each is described briefly below. They are considered collectively under the term *cline* in the sense of HUXLEY (1940).

Solenopsis s. cline saevissima-richteri

1. Var. *moelleri* Forel. This includes the darker forms found just south of the range of the typical *saevissima*. As mentioned above, their color differs from that of *s. saevissima* only in shade. They cannot be considered as constituting a distinct subspecies because they represent a clinal nuance of the typical subspecies, approach true intergrades between this subspecies and *s. richteri*, and occupy too poorly defined a range.

2. The Bolivia variant. This form is very similar to *moelleri*, but with the head exclusive of the occiput much lighter than the rest of the body and creating an almost bicolored appearance. It is apparently a local clinal form.

3. Subsp. *electra* Forel. This variant is characterized by a flattening in the soldiers and larger medias of the dorsum of the alitrunk, with a coincident elongation of the propodeum. The condition is connected with the typical arcuate forms by graded intermediates. The color is highly variable, ranging from light reddish brown to piceous brown. CREIGHTON was of the opinion that transverse striation of the entire declivious face of the propodeum was another diagnostic feature of this form, but this has not proven to be the case.

4. Light red phase. This variant is apparently identical with the "light red phase" of the introduced Gulf States population (Fla., Ala., Miss.), which has previously been described in some detail (WILSON, 1951). In the Gulf States it occurs with the typical *saevissima richteri*, and both forms intergrade extensively. During the past twenty years it has largely replaced both the *richteri* and the intergrades and has been responsible for the explosive spread of the species. In Argentina the light red phase is surrounded by forms which differ in very minor ways, such as the possession of a lighter ground color and the occurrence of a faint gastric patch in the soldiers and large medias. Its common occurrence in northern Argentina seems to strengthen greatly the possibility that it reached the Gulf States through a second introduction instead of by a series of mutations within the first population. It should be noted that the introduced population contains an equivalent segment of the blend zone population. In the introduced population the variation extends only between two extremes. It has the appearance of, having originated from two genotypes which were separated from one another by a small series of alleles. These genotypes interbred completely to give a genetic picture which may have been as simple as the following: AAAA, AAAa, AaAa...aaaa. Natural selection through biotic pressure has operated to swing the balance strongly toward one end of this series.

5. Intermediate phases. These include the light intermediate and intermediate phases described in detail previously (WILSON, 1951). They appear to be straight intergrades between the light red phase and typical *saevissima richteri*.

In addition to these local variants there are two synonymized forms of less certain distribution which deserve special mention. SANTSCHI's subsp. *oblongiceps* was described from three workers collected at Loreto, Misiones, which is near the center of the *saevissima-richteri* blend zone. The characters which SANTSCHI proposed utilized features which are among the most variable in the species, including thickness of the petiole and placement of the clypeal carinae. The most diagnostic character given was the elongate head of the two largest workers, but the figure accompanying the description shows a head which is not at all extraordinarily elongate. The head can be described at the most as being relatively slender and subquadrate, a condition common in blend zone material. In addition, the color of the types as given by SANTSCHI corresponds very closely to that of the several series from Loreto which I have examined. Although the SANTSCHI types are at present unavailable, I feel little hesitation in eliminating this form on basis of the description alone.

The status of SANTSCHI's var. *perfida* is not quite so easily settled. It was described from Piracicaba, Minas Gerais, well within the range of the typical subspecies. The diagnostic characters given were sixth and seventh funicular segments as broad as long, and head of minors not perceptibly narrowed behind the eyes. The first character is a relatively variable one in *s. saevissima*, and *perfida* may well represent only one extreme. Although I have never seen minors of the typical race with quadrate heads, this second character does occur commonly in the blend zone. Thus it would be very unwise to recognize *perfida* as a distinct species, while its distribution precludes the possibility of its representing a distinct subspecies. Perhaps examination of additional Brazilian material will show this variant to be more common and of closer affinity to *s. saevissima* than is now evident.

Solenopsis saevissima richteri Forel

- 1909 *Solenopsis pylades* var. *richteri* Forel, Deutsche Ent. Zeit., p. 267. Type locality: Buenos Aires, Argentina.
- 1912 *Solenopsis pylades* var. *tricusps* Forel, Mem. Soc. Ent. Belg., Vol. XX, p. 4.
- 1913 *Solenopsis pylades* var. *quinguecusps* Forel, Bull. Soc. Vaud. Sci. Nat., Vol. XLIX, p. 224.
- 1915 *Solenopsis geminata* subsp. *saevissima* var. *quinguecusps* Forel, Wheeler, Bull. Amer. Mus. Nat. Hist., Vol. XXXIV, p. 397.
- 1915 *Solenopsis geminata* subsp. *saevissima* var. *richteri* Forel, Wheeler, *Ibid.*, p. 397.

- 1915 *Solenopsis geminata* subsp. *saevissima* var. *tricuspis* Forel. Wheeler, *Ibid.*, p. 397.
1916 *Solenopsis saevissima* var. *quinquecuspis* Forel. Santschi, *Physis Buenos Aires*, Vol. II, p. 281.
1916 *Solenopsis saevissima* var. *richteri* Forel. Santschi, *Ibid.*, p. 281.
1916 *Solenopsis saevissima* var. *tricuspis* Forel. Santschi, *Ibid.*, p. 281.
1950 *Solenopsis saevissima* subsp. *richteri* Forel. Creighton, *Bull. Mus. Comp. Zool.*, Vol. CIV, p. 232.

This subspecies varies from dark to piceous brown; a light reddish patch on the anterior dorsum of the first gastric segment may or may not be present. It is the southernmost population of the species, and it is relatively homogeneous over its limited range.

DISCUSSION

Although the variation in *Solenopsis saevissima* has been difficult to resolve into taxonomic categories, it should be of exceptional interest to the systematist as an example of incipient continental subspeciation. As mentioned previously, the species exhibits a north-south cline in at least two characters. Color, which is one of these characters, is used in defining the two recognized subspecies, but only because the distinctive color of each is relatively widespread, homogeneous, and peculiar to a circumscribe area. This view is strengthened by the erratic variation, both in color and body proportions, which occurs in the broad zone of intergradation. Here numerous minor variants occur which tend to be local. These well may represent incipient subspecies in themselves; for instance, the Bolivia variant may be evolving as a race peculiar to Bolivia and northwest Argentina, and subsp. *electra* or the light red phase may eventually come to predominate in north-central Argentina and Paraguay. At the present time all of these variants possess color characters clearly intermediate between *saevissima* and *richteri*, and they overlap in distribution to such an extent as to preclude their recognition as valid subspecies. In addition to this erratic divergence in color and body proportions, the entire population in the zone of intergradation also tends to differ in size. As CREIGHTON demonstrated in 1930, the forms now recognized as intergrades are considerably smaller than either subspecies, in both the worker and queen castes. I have treated statistically this size difference between *richteri* and the light red phase and shown that it applies to all three castes, with the means increasing stepwise from the latter to the former through intermediates (WILSON, 1951). This represents what may be considered a separate clinal trend which reverses itself in the center of distribution, and it may indicate an independent divergence of the blend zone population as a whole.

A careful examination of the variation *S. saevissima* shows that the present delimitation of the ranges of the two subspecies is a some-

what arbitrary one, primarily because of the extend and complexity of the blend zone. The variation becomes understandable only if a more dynamic concept is applied. The species appears to be in an early stage of subspeciation, in which large segments of the population are reaching adaptive peaks and relative homogeneity. The clinal nature of much of the variation is possibly the original condition. It has remained to overshadow the divergence of the young subspecies, which are acquiring diagnostic characters of a nonclinal nature.

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